

The phenomena of disorganization.¹

The earlier researches regarding the death of the plant-cell have taken account chiefly of the dynamic sources of disorganization, such as heat, light, electricity, and given little attention to the material sources. Moreover they have largely overlooked the fact that the plant does not surrender its life without a fight, often of relatively long duration, which finds expression in the extraordinary internal alterations that are manifested whether the cell triumphs or surrenders, whether the disorganization is reparable or irreparable. The later researches have proceeded chiefly along two distinct lines, from the standpoint of the chemist and that of the physicist. The one views the cell-organism as essentially a chemism, the other as a mechanism. The researches of Loew and Bokorny are of the first sort, those of Berthold and of Bütschli of the second. Viewed thus the real characteristic of the organism, viz., the interdependence of the cycle of processes making up life (processes which we distinguish as chemical and physical), is put too far into the background. To the one the organism appears too much as a machine, to the other too much as a vessel in which chemical reactions are occurring. Rather we must consider the organism neither one nor the other, but that, as chemical and physical processes go hand in hand, we have before us a metabolic energy-transforming complex (*Stoff-Kraftwechselsystem*) comparable rather to a factory than to a machine.

Klemm determined to observe and compare the phenomena which became visible under the action of disorganizing media of known character applied designedly, and to see whether the likeness and difference in the death phenomena were merely superficial or were of deeper significance, depending upon the nature of the disorganizing agent. By choosing the proper amount or strength of the material or dynamic agent, and thus making the transition from life to death slow, Klemm endeavored so to arrange his experiments as to observe as many as possible of the phases of disorganization. It seemed specially important also to prove how the cells behaved under the gradual intensification of an agent up to an injurious degree as compared with the sudden application of the same agent of like intensity, so as to be able to distinguish clearly

¹KLEMM, PAUL: Desorganisationserscheinungen der Zelle. *Pringsh. Jahrb. f. wiss. Bot.* 28: 627-700. *pl. 2.* 1895.

the characteristic action of the agent from the reaction due to the sudden change of conditions. Great variability is to be expected not only according to the plant, but even among like cells of the same plant, and at different times and under different circumstances.

The symptoms of death are in most cases distinct enough, but in doubtful cases death was determined by the incapability of contraction on the addition of a plasmolyzing solution, or by the capacity to accumulate coloring matter, which appears only at death. Nigrosin, which is entirely harmless, was chiefly used for this test.

As dynamic agents Klemm used high and low temperatures, light, and electricity. As material reagents he used inorganic and organic acids, alkalies and alkaloids, H_2O_2 , $CuSO_4$, $FeSO_4$, alcohol, phenol, and anilin colors.

As experimental material, that specially rich in protoplasm proved most serviceable, such as plasmodia of Myxomycetes, stamen-hairs of *Tradescantia*, cells of *Spirogyra*, filaments of *Vaucheria* and some marine Siphonææ, hyphæ of *Saprolegnia*, and the root hairs of *Trianea Bogotensis*, which are finely adapted to the action of material agents because not cuticularized.

1. *Heat.* Previous observations mainly agree as to the visible alterations from high temperatures, viz., cessation of movement, rigor, and eventually aggregation or separation of masses of protoplasm. Klemm used Pfeffer's warm stage and determined, first, that gradual heating can be carried to a degree at which its sudden application is immediately fatal. Under these circumstances the alterations affect the movement rather than the form of the protoplasm. The first effect of heating beyond the optimum is to produce a condition of irritation marked by a feverishly rapid streaming. At a yet higher temperature the streaming was slowed with often tremulous movements of the plasma strands. This was succeeded by the formation of clumps here and there, and later by rigor. Hairs of *Momordica* and *Tradescantia* could be heated gradually to 51° without death. Contraction of the plasma from the wall followed, but when heat was applied suddenly no contraction took place. Killed in this way a strikingly granular appearance was imparted to the protoplasm. When heat is continuously increased turgor does not diminish until the death begins. By applying a heat of $42-45^\circ C.$ at once

the internal revolution described by Sachs could be obtained; but it is readily shown that the plasma regains something of its original form if kept at this temperature, while if cooled the alteration of form becomes complete. The effects therefore are effects of change, not specifically of heat. Heat itself works disorganization without characteristic deformation, except the appearance of granulation in the last stage.

Low temperatures within the minimum showed essentially like effects. Only a sudden change produced any substantial deformations. Contractions of the plasma occur in considerable amount only at temperatures which after longer time produce death. These, therefore, are only the expression of the general injury, not the specific and immediate effects necessarily accompanying disorganization by abnormal temperature, which are purely internal and molecular and are expressed only by the granular appearance of the protoplasm killed by extreme temperature.

2. *Light.* No attempt was made to determine whether a lower limit exists, though the experiments of Hofmeister and Baranetzky mentioned in Pfeffer's *Physiologie* suggest such a possibility. Pringsheim established the fact that a high intensity of light can disorganize and kill protoplasm. But Klemm was not able to discover any phenomena which are typical of death through light, either because they occur exclusively or in higher degree under its action. Light, however, is not able to produce such intensive mass movements, when suddenly applied, as does heat suddenly applied.

3. *Electricity.* The disorganization produced by electricity, however, is of an entirely different character from that by heat and light, consisting of phenomena of solution which lead to the swelling of the protoplasmic layers and strands and to an extraordinary formation of vacuoles. The alterations mentioned in the older literature therefore are only the beginnings of the action which find outward expression especially in the streaming plasma—only the gross deformations which perhaps have their origin chiefly in the mechanical action of the induction shock, while the peculiarity of the electrical action lies in the internal changes it produces, leading to a frothy vacuolization of the plasma. This is made even more evident when the motion of the plasma is previously checked by withdrawal of oxygen or by chloroform.

4. *Reagents.* Acids produce, as characteristic disorgani-

zation phenomena, a granulation pointing to precipitates in the protoplasm, and a rigor, without any considerable contraction. It is this which has made them useful as fixing reagents in microtechnique. Alkalies and alkaloids disorganize by producing an abnormal solubility of the constituents of the protoplasm, so that it becomes vacuolated like a mass of foam, thus resembling in effect electric currents.

With hydrogen peroxide an extremely fine fibrillar structure of the plasma was produced, the fibrils mostly running lengthwise, a few transversely, and either ending free or joined into a network. Even the nucleus appeared not simply granular but like a coil of fibrils. The metallic salts produced no visible changes of structure or configuration. Anilin stains bring about an aggregation of the protoplasm as Pfeffer showed. Klemm sought to observe the fate of the cell after aggregation and to determine whether it is capable of life in spite of the experience which the mass of the cytoplasm has undergone, and whether, perhaps, the extruded balls are again taken up into the plasma. Though he used the large rhizoids of *Chara* he was not able to see that the cells had suffered any considerable injury, nor that the balls were again taken up into the plasma, though they were many times crowded deep into it. The balls themselves retained their life for a long time.

Summarizing his results Klemm says: In disorganization produced by forces and substances there is no single visible phenomenon common to all. The separate alterations to be observed are: *collapse* of the protoplasm, in which the diminution of turgor finds expression, *deformation* consisting of gross alteration of contour and separation of parts of the protoplasm, and finally *structural alterations* in the protoplasm.

1. That many agents at the very beginning of disorganization produce a diminution of turgor, either by changing the cell-sap or the resistance of the plasma to filtration, is certain. Yet this rarely goes so far as to produce real contraction, severing the protoplasm from the wall as in plasmolysis. After death turgor is, naturally, always diminished; yet irregular contraction, collapse, never appears; nor does it as a specific effect of any disorganizing medium. On the contrary collapse may or may not take place with any agent. Whether it will or not depends on the degree of harmfulness. The more harmful, whether on quantitative or qualitative

grounds, the less does the plasma collapse. Thus, no collapse occurs with a high intensity of light or heat, a high concentration of alcohol or acids, while on the contrary it does occur with low intensity or concentration. By no means all agents tend to diminish turgor; an increase even, of osmotic pressure is not excluded.

2. Alterations of configuration, such as formation of nodules, aggregation, separation of protoplasm, are a consequence of the sudden intensive action of many agents. They are wanting on the gradual application of agents to an amount or degree equal to that at which a sudden application produces such deformations. Alterations of internal movement to external recognizable mass movements go on only when agents are introduced suddenly.

3. Alterations of internal structure of protoplasm are not to be observed in all disorganization. When recognizable at all they fall into three categories: (1) Secretions of various forms, principally small grains which give to the plasma, in comparison with the normal, a much more granular appearance. They may be united into chains, nets, dendritic and other groups. These secretions may even take the form of fibers and impart a fibrillar appearance to the plasma. (2) Phenomena of solution which manifest themselves in the formation of vacuoles. In consequence of this vacuolation the plasma may be completely transformed into a foam. The vacuoles may be of considerable size but in part they lie near the limit of microscopic observation. This action is typical of basic substances and appears generally in consequence of electric shocks. (3) Coagulation of the plasma with granulation and formation of vacuoles, few and of small size. This occurs in many cases, especially in mechanical destruction of the protoplasm.

The alterations of the nucleus are in general completely analogous to those of the cytoplasm.

The structures of the protoplasm observed by different investigators, reticular, fibrillar, alveolar, are not permanent structures of high physiological significance but are only different states, producible at will in one and the same protoplasm.—C. R. B.